

MCCOSKERICHTHYS SANDAE, A NEW AND UNUSUAL CHAENOPSID
BLENNY
FROM THE PACIFIC COAST OF PANAMA AND COSTA RICA^{1,2}

by RICHARD H. ROSENBLATT³ AND JOHN S. STEPHENS, JR.⁴

ABSTRACT: A new genus and species of chaenopsid blenny is described, based upon a series of 651 specimens. This new species occurs at depths ranging from 1 to 30 meters along the Pacific coast of Costa Rica and Panama. It is a tube dwelling blennioid fish, living along near-vertical rock faces or coral heads. This new chaenopsid is unique in having the following combination of characters: four circumorbital bones, ectopterygoid teeth, jaw with spatulate teeth on outer row but granular ones on inner row, five orbital cirri, a blunt head, 17-20 spines and 31-34 soft rays in dorsal fin, 2 spines and 32-36 soft rays in anal fin, and 54-57 vertebrae. The relationships of the new genus are discussed as they relate to the clinidlike blenny families (Clinidae, Chaenopsidae, Tripterygiidae). Osteological features are discussed and illustrated, and their interpretation as evidence of evolutionary significance is presented.

INTRODUCTION

In 1971 while on fellowship to the Smithsonian Tropical Research Institute in Panama, John E. McCosker collected and made observations on a new species of tube dwelling blennioid fish. Extensive series of this species were also taken by McCosker and Rosenblatt during the Janss Foundation expedition to Costa Rica on the R/V *SEARCHER*. The characteristics of this species are so distinctive that it cannot be assigned to any known genus, but its characteristics certainly ally it to the family Chaenopsidae.

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Mccoskerichthys NEW GENUS

Figure 1

Diagnosis: A chaenopsid with the following unique combination of characters: four circumorbital bones, teeth on the ectoptergoid, outer row of jaw teeth spatulate, teeth of inner rows granular, 5 pairs of orbital cirri and a combination of blunt head and high dorsal, anal and vertebral counts. Other characters those of the single included species.

Type species: *Mccoskerichthys sandae* new species

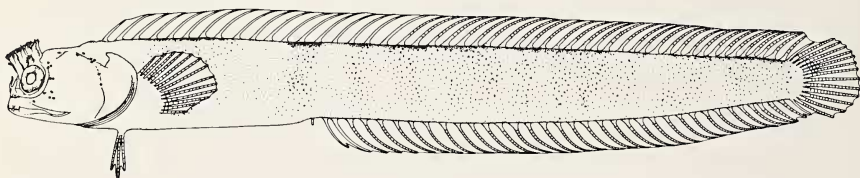
Derivation of name: Named for John E. McCosker, who discovered the species and has participated in the collection of all known specimens.

RELATIONSHIPS

Böhlke and C. H. Robins (1974) in describing the new clinid genus *Haptoclinus* discussed certain characters of this monotypic genus that they regarded as breaking down the separation of the three often recognized clinidlike blenny families: the Clinidae, Chaenopsidae and Tripterygiidae. They recognized only the family Clinidae, admitting that the chaenopsids and tripterygiids represent lines of divergence within the family, but suggested that other equally distinct clinid subgroups may later be defined. However, the characters given for *Haptoclinus apectolophus* do not seem to indicate relationship to chaenopsids; in fact, all its characters are typically clinid. There is also very little evidence presented allying *Haptoclinus* to the tripterygiids. *Haptoclinus* represents a specialized clinid, perhaps allied to *Paraclinus*.

It may well be that uniting all clinidlike or clinid-derived fishes into a single family is the best way to treat these relationships but unfortunately the discussion by Böhlke and Robins (1974) is mostly irrelevant to this problem. We, therefore, will continue to treat clinids, chaenopsids and tripterygiids as separate blennioid families.

The morphological characters given in the diagnosis of *Mccoskerichthys* indicate its isolated position within the family Chaenopsidae. Any one of these characters distinguishes this genus from all other known chaenopsids, and the presence of ectopteryoid teeth is unique within the Blennioidei. If these special characters are ignored, *Mccoskerichthys* seems to be most closely related to the *Protentemmaria* to *Acanthemblemaria* line of chaenopsids in that the paired nasals have fused medially into

FIGURE 1. *Mccoskerichthys sandae*, Holotype

a single element and the frontals (parietal of Jollie 1962; Stephens 1963) are ridged and sculptured (Fig. 3). Further, there is a tendency toward modified dentition in this evolutionary line. The species of *Chaenopsis* agree with *Mccoskerichthys* in having a high number of vertebrae and dorsal and anal soft rays, as well as the correlated characters of a reduced number of caudal peduncle vertebrae and the absence of dorsal pterygiophores anterior to the first vertebra, but are otherwise very different.

Stephens (1963) listed 13 characters he considered to represent the primitive condition in chaenopsids. *Mccoskerichthys* exhibits the primitive condition in six characters (snout shape, orbital cirri, palatovomerine dentition, upper jaw length dimorphism, median fin height and circumorbital width). Although relatively slender circumorbitals were considered to be primitive by Stephens, this character needs clarification. The primitive condition is better described as a slender lachrymal and the advanced character a ventrally expanded lachrymal as in most *Coralliozetus* (σ σ) and most species of *Acanthemblemaria* (Figs. 6-9). The other circumorbitals are relatively stout primitively (Stephens 1963, fig. 2A and B). The slender circumorbital ring is found in almost all species of the *Emblemaropsis* to *Chaenopsis* line, though several species of *Emblemaria* show a modified, stouter ring. The circumorbital ring of *Mccoskerichthys* is similar to that of *Neoclinus*, a clinid considered close to the ancestral chaenopsid lineage, in that there are four bones, the lachrymal is slender and

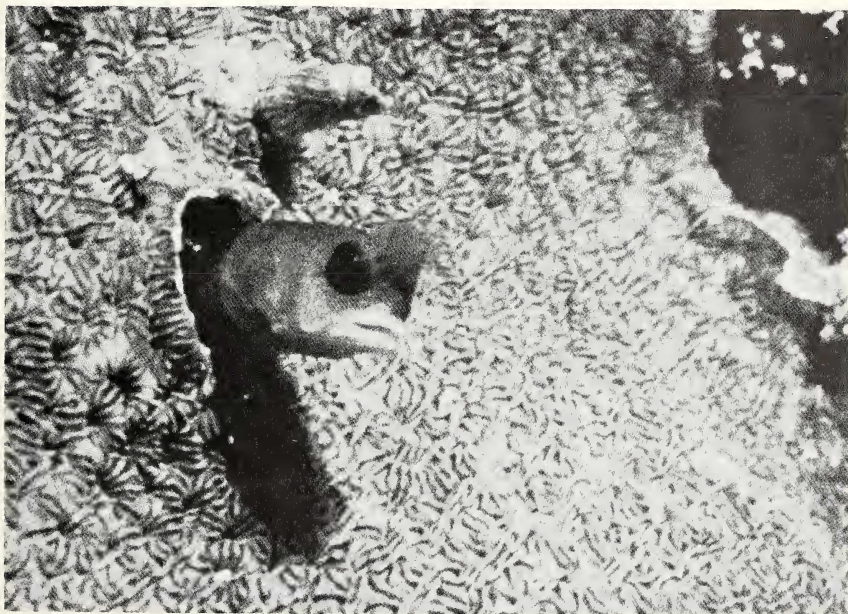


FIGURE 2. *Mccoskerichthys sandae*, a living individual in a tube in the coral panona. Photo taken by Edwin Janss at Isla del Caño Costa Rica in March, 1973.

the other three circumorbitals (postorbitals) relatively stout. *Neoclinus* has a distinct dermosphenotic not present in *Mccoskerichthys* or other chaenopsids.

The four circumorbitals, blunt snout and low nondimorphic dorsal fin impart a primitive facies to *Mccoskerichthys*. The strongly modified dentition, presence of teeth on the ectopterygoid, and the elongate body are specializations but do not argue against a primitive origin. If the presence of four circumorbital bones indeed represents the retention of a primitive character, then *Mccoskerichthys* must have evolved prior to the division of the chaenopsids into the *Protemblemaria* to *Acanthemblemaria* and *Emblemariopsis* to *Chaenopsis* lineages, as the circumorbitals are reduced in both. If *Mccoskerichthys* diverged this early, however, it is difficult to explain its numerous apomorphic characters shared with members of the *Protemblemaria* to *Acanthemblemaria* lineage, i.e. a single fused nasal, cranial sculpturing, specialized incisor and molariform dentition, as well as short and stout pelvic fins.

Mccoskerichthys is certainly not particularly clinidlike: the body is scaleless, and the lateral line absent, most of the head pores are simple, there is a single epural, and the fifth hypural (minimal hypural) is not identifiable nor are the dermosphenotic and median and lateral extrascapulars. All of these are chaenopsid characters. Typically there are two epurals and the fifth (minimal) hypural in the Clinidae and the dermosphenotic and one or more extrascapulars are present. It must be stressed, however, that the chaenopsid condition in these osteological characters is approximated by *Stathmonotus* and *Starksia* and in one or more characters by other clinids. An additional chaenopsid character, the presence of a well defined anteriorly projecting lateral process on the hyomandibular (Figs. 6, 7, and 9) has been examined by Springer (personal communication). This hook is certainly characteristic of most species but appears to be absent in *Coralliozetus* (Fig. 8) and those species of *Emblemariopsis* that we have examined. This process is at best rudimentary in *Mccoskerichthys* (Fig. 3).

It is difficult to evaluate the phyletic significance of the presence of four separate postorbital bones in *Mccoskerichthys*. It would be especially helpful to know whether there are three postorbital centers of ossification or only one in the rest of the chaenopsids. If there are three, joints could easily be regained; if one, it is likely that the separate bones of *Mccoskerichthys* represent a primitive condition. The fact that the postorbital of other chaenopsids anomalously may show separate elements suggests that several centers of ossification are present and that these normally fuse during development.

It is our interpretation, based on parsimony, that *Mccoskerichthys* evolved after the main chaenopsid features had appeared, and that it represents an offshoot of the *Protemblemaria* to *Acanthemblemaria* line close to *Ekeblemaria* in the phylogenetic diagram given by Stephens (1970) but has lost the fusion of the postorbitals. This phyletic position eliminates the difficulty of interpreting the synapomorphies of the *Mccoskerichthys* and the *Protemblemaria* to *Acanthemblemaria* species.

Mccoskerichthys also agrees with the Chaenopsidae in another feature, which has not previously been noted. In chaenopsids the maxilla is not visible externally. Anteriorly it slips beneath the lower free margin and posterior projection of the lachrymal (the postorbital or second circumorbital usually forms the dorsal parts of the projec-

tion). Posteriorly, a free fold of skin extends from the posteroventral angle of the circumorbitals across the cheek forming a pocket covering the maxilla. This pocket is variously developed but present in all species. It is best developed in *Chaenopsis*, in which the maxilla extends far beyond the rear margin of the eye, and least developed in forms where the maxilla is short or the posterior expansion of the circumorbital ring is large. In *Mccoskerichthys* the posterior extension of the lachrymal and the second circumorbital cover all but the posterior tip of the maxilla and the free fold is rudimentary. *Emblemaria* has a reduced fold, but the maxilla is buried beneath the skin and there is a fold across its tip. This character is approximated in some genera of clinids including *Stathmonotus* and *Malaccoctenus* but not *Haptoclinus*.

The effect of these structural chaenopsid modifications is to limit the lateral expansion of the jaws. Because of the limited protusibility of the premaxilla, the maxilla is but little rotated downward when the mouth is opened. Illustrations of throat display in which the mouth is opened widely in *Chaenopsis* and *Emblemaria* (Robins, Phillips and Phillips 1959, text fig. 1, Pl. 3, figs. 1 and 2; Wickler 1964) indicate that the maxilla remains closely applied to the cheek. The rigidly fused circumorbital ring of chaenopsids further limits lateral mobility of the maxilla.

It is possible that the early chaenopsids were omnivorous nibblers, and that the change to plankton-picking, characteristic of most members of the family (species of *Coralliozetus*, *Acanthemblemaris*, *Protemblemaria*, and *Emblemaria* examined, see also Stephens, Hobson and Johnson 1966; Hobson 1968) was correlated with increasing reliance on the tubiculous habit. *Chaenopsis* and *Lucayablennius* (Hobson 1968; Greenfield 1972) have become predators on relatively large food items, and the gape is proportionately long, but the basic chaenopsid jaw structure is otherwise little modified. The chisel-like teeth of *Mccoskerichthys* hardly seem adapted to plankton feeding, yet observations and gut analyses suggest this mode of existence.

Mccoskerichthys sandae NEW SPECIES

Figures 1, 2

Morphology: Terminology is that of Stephens 1970. Counts and measurements of certain body parts are given in Tables 1 and 2. Body greatly elongated for a chaenopsid, approaching the species of *Chaenopsis* in this respect, body depth at dorsal origin 10-12 in standard length. Body strongly compressed; its dorsal and ventral outlines with little posterior taper. Head length 5.5-7.0 in standard length, head width slightly less than its depth. Snout short and rounded, lips projecting because of broad, projecting incisors; snout length from two-thirds of, to almost equal to, eye diameter, difficult to measure accurately, because of anterior excavation of orbit. Eyes directed anteriad as well as laterad, pupil round; diameter of eye 3.5-4.5 in head. Interorbital narrow, rim of orbit incised anteriorly to accommodate anteriorly directed eyes, and posteriorly to accommodate orbital cirri. Orbital cirri forming a bushy mass, which completely covers interorbital region. Cirral mass composed of five pairs of cirri; each cirrus with a stout base and at least two major branches, one medial and one lateral, each branch complexly multifid and with short lateral branches, imparting a ragged

TABLE 1
Meristic variations in
Mccoskerichthys sandae.

Total Dorsal Elements				
50	51	52	53	
8	19	14	6	
Dorsal Spines				
XVII	XVIII	XIX	XX	
4	12	26	5	
Dorsal Soft Rays				
31	32	33	34	
3	17	19	8	
Anal Soft Rays				
32	33	34	35	36
1	1	23	21	1
Pectoral Rays*				
12	13	14		
5	85	2		
Total Vertebrae				
54	55	56	57	
6	32	12	4	

*2 damaged pectoral fins with 10 and 11 rays

appearance. Cirral mass extends from posterior edge of postorbital flange of frontal to anterior margin of eye at level of center of pupil; height of mass slightly less than eye diameter.

Top of head behind eyes with a series of transverse folds, which become longitudinal and converge toward dorsal commissural pore; folds originate anteriorly about at junction of frontals with circumorbitals and reflect underlying bony ridges. A crescentic fold at occiput, outlining anterior extent of body musculature. Fold reduced in females and absent in juveniles, although bony ridges may be seen.

Upper jaw horizontal, terminating behind eye, its length about 1.3-1.5 in post-orbital head length. Maxilla in males extending slightly beyond end of posteroventral expansion of circumorbitals, rather than ending beneath it as in females. Upper jaw with a pair of recurved incisors, one on either side of symphysis, followed by three enlarged, somewhat forward-directed, spatulate incisors; posterolateral to these a row

TABLE 2

Measurements in millimeters of body parts of the holotype and ten paratypes of *Mccoskerichthys sandae*

	<i>Holotype</i>											
Standard length	62.5	63.5	65.0	69.5	62.6	59.9	62.5	62.0	69.1	65.7	65.0	
Head Length	10.0	9.6	10.0	10.0	9.7	9.9	9.6	9.6	9.3	9.6	9.5	
Head Depth	5.5	5.1	5.6	5.9	5.0	4.9	5.5	5.1	5.6	5.4	5.5	
Head Width	5.4	5.3	5.7	5.5	5.0	5.1	5.9	5.4	5.8	5.4	5.1	
Upper Jaw Length	4.9	4.3	4.5	4.5	4.5	4.9	4.9	4.0	5.0	4.6	4.4	
Snout Length	1.9	1.7	1.9	2.0	1.6	1.6	1.9	1.9	1.9	1.9	1.5	
Eye Diameter	2.1	2.3	2.1	2.0	2.0	2.3	2.1	2.1	2.0	2.3	2.1	
Interorbit Width	.9	.9	.9	.9	.8	.7	.7	.6	.8	.6	.7	
Predorsal Length	8.0	7.9	7.9	8.5	7.9	8.0	8.0	7.9	8.0	8.0	7.8	
Preanal Length	25.5	25.0	26.1	27.8	24.6	24.5	25.0	25.4	26.0	27.0	25.6	
Body Depth at Anus	5.7	4.8	5.3	5.2	4.9	4.8	5.5	5.6	5.6	5.0	5.5	

of 7-10 smaller, downward directed, stout incisors. A patch of granular teeth anteriorly behind large incisors, continued as a single row behind small incisors. Dentition of lower jaw similar to that of upper except that there are no small symphyseal incisors, and there is a pair of stout, conical, almost caniniform teeth, one on each side of symphysis, behind patch of granular teeth. About 6 short, stout, teeth on vomer. Palate with a patch of teeth anteriorly on palatine, narrowing to two rows posteriorly; ectopterygoid with a zig-zag row of ten teeth. Anterior nostril just above upper lip, with a short tube bearing two tentacles on its rim, one anterior and one posterior. Posterior nostril just behind anterior. Cranial sensory pores mostly simple, except over postorbital bones; preoperculo-mandibular series with 1 commissural, 3 occipital, 1 lateral, and 1 temporal, 6-7 preopercular and 5 mandibular anterior to corner of mouth; postorbital series with 2 pores; supraorbital series with 4 pores. No pores on body posterior to upper corner of gill opening.

Gill membranes united, free from isthmus; branchiostegals 6. Gill rakers 4-5+11-12 on first arch in five specimens counted.

Total dorsal fin rays 50-53; XVII-XX, 31-34. Dorsal origin above upper anterior corner (formed by attachment of opercle membrane to body) of operculum. All rays evenly spaced, first spine short, two-thirds length of second, subsequent rays subequal, with middle of soft dorsal somewhat higher; longest soft rays $1.5 \times$ first and last soft rays.

No notch between spinous and soft dorsal, last ray attached for its entire length by a membrane inserting on middle third of dorsalmost segmented caudal ray. Anal fin II, 32-36, all soft rays evenly spaced, spines slightly closer together. First spine short, one-half length of second, and one-third as long as first soft-ray. Soft-rays subequal, last ray attached as last dorsal ray but to ventralmost procurent caudal ray. Caudal rounded, with 13 segmented rays and 3-6 procurent rays; only one procurent ray visible dorsally and one ventrally. Pectorals rounded, about 1.5 in head length, rays 12-14. Pelvics short, about two-thirds pectoral length, 1, 3, spine short, closely

applied to first soft-ray, soft-rays joined by membrane, middle ray longest. Male with a well-developed, fingerlike genital papilla, female with numerous short, flattened, fleshy processes around anus, and a short, broad genital papilla.

Osteological characteristics: The important cranial and caudal characters of *Mccoskerichthys sandae* are presented in figures 3-5. Comparative illustrations of *Protemblemaria* to *Acanthemblemaria* are presented in figures 6-14. Worthy of note for *Mccoskerichthys* are: the specialized anterior dentition, well-hidden maxillary, posteroventrally expanded circumorbital ring; 3 postorbital elements; fused nasals, sculptured frontals; single epural oriented almost vertically; absence of distinct minimal hypural; close association of last dorsal and anal pterygiophore to caudal (3 vertebrae between urostyle and last pterygiophore). Two additional osteological characteristics of this species that may be worthy of note are the presence of 3 anal pterygiophores anterior to the first haemal arch (typical of chaenopsids) and the lack of any dorsal pterygiophores anterior to the first vertebra (all chaenopsids except *Chaenopsis* have 2-3 pterygiophores anterior to the first vertebra).

Color in alcohol: Males are dark brown to tan with a series of darker marks on the sides. The dark markings vary from squarish or almost circular blotches to bars. When blotches are present there is usually a series of about 8 along the dorsal base and a series of 10-12 more or less centered on the midline. When bars are present there are usually about 10-12. The bars are irregular, and may be split by light centers. The head is notably lighter than the body, but there is much variability. In some individuals only the snout, jaws and lower surface of the head are much lighter than the sides. The cheeks and opercles are usually darker than the anterior and ventral parts of the head. The orbital cirri appear pale, but are dusted with melanophores. Often the light coloration of the head extends onto the body and there is a sharp line of demarcation extending from the pectoral base to the dorsal, between the third and fourth spines. The line of demarcation is accentuated by a dark bar behind the fourth dorsal spine. The belly is dusted with chromatophores and varies from lighter than the sides to almost as dark as them. The folds around the anus are outlined in black and the genital papilla is contrastingly white. There is much variability in coloration: in some individuals the body is light with the dark markings strongly contrasted, in others the body is dark brown and the markings difficult to discern. This variation in coloration is not correlated with size, but may be related to breeding condition.

The median fins are clear, except that the dorsal fin is marked with brown for the first 3-5 spines. The pectoral has a dusky area basally and the pelvics usually have a few melanophores on them, mostly basally.

Females are similar to males in coloration, but the head, orbital cirri and belly are paler, and a higher proportion have pale background color. However, dark females and light males do occur. In life the impression is of a dark red fish with the light areas light olive green. The dark body markings are vague, and all the fins are red.

Ecology: *M. sandae* occurs along near-vertical rock faces or coral heads, in areas of moderate surge, where they inhabit mollusc or worm tubes. The heads protrude from the tubes, and the fish make short darts forward, apparently snapping at plankton. Individuals were not seen to emerge completely from their tubes, but may come out

for one-half the body length or more. The elongated body of *M. sandae* allows the head to be thrust well away from the tube in feeding, with the tail still in contact with the substrate. Stephens et al. (1966) indicated that *Acanthemblemaria macrospilus*, a relatively short bodied species, may leave its tube in feeding.

Observations indicating that *M. sandae* feeds on plankton were confirmed by the examination of gut contents of several specimens. Most individuals contained fragments of copepods and amphipods, and occasional ostracods. Individuals from LACM 32551 contained numbers of tiny (.3-.5 mm) planktonic stages of pelecypods and gastropods.

M. sandae has been taken at depths ranging from 1m (3 ft) to almost 30 meters (100 ft). The shallowest records were from the Gulf of Chiriqui, Panama; at Isla del Caño, Costa Rica; individuals were not seen much shallower than 5 meters (15 ft).

There was a striking disparity in the numbers of males and females in the Costa Rica collections SIO75-404 (capture depth 5-10 m) contained 149 males and 76 females. LACM 32551 (capture depth 20-30 m) yielded 231 males and 154 females. The ratios of males to females deviate from 50:50 at $p < .01$. This unbalanced sex ratio in favor of males is difficult to explain. It almost certainly does not represent unisexual patchiness. The areas collected were large, and the tube-dwelling habit, small size and relatively poor swimming ability of the species makes it unlikely that the sexes could come together for breeding if they did not live in close proximity. It is possible that collecting bias toward the more obvious specimens could be involved, since males reach a larger size than females. This cannot be ruled out, but it is not likely that the great disparity in sex ratios can be attributed to it.

Otoliths were removed from three specimens before preservation (63.0, 66.0 and 69.5 mm). The otoliths were cleared in anise oil and examined by John E. McCosker. The largest and smallest specimens had three hyaline rings, the outer at the margin, indicating that they may have been entering their fourth year of growth. The 66.0 mm individual did not have differentiated areas in the otolith.

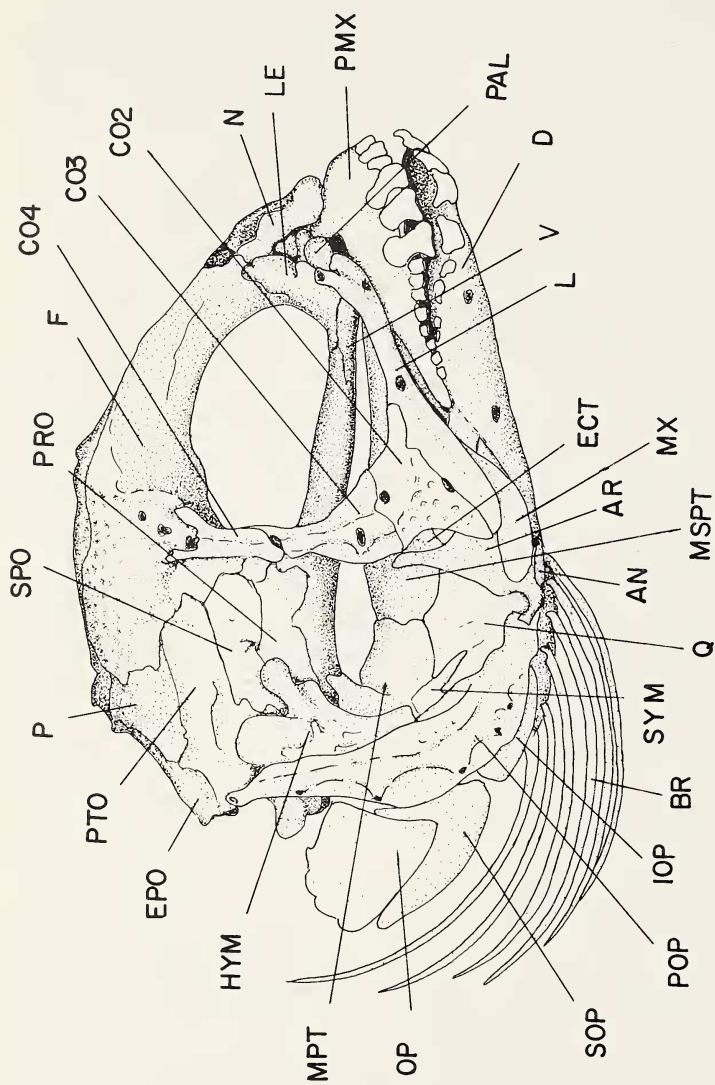
Range: Thus far known only from Isla del Caño, Costa Rica and the Golfo de Chiriqui, Panama.

Derivation of name: Named for Sandra McCosker, who participated in the first collection of the species.

MATERIAL EXAMINED

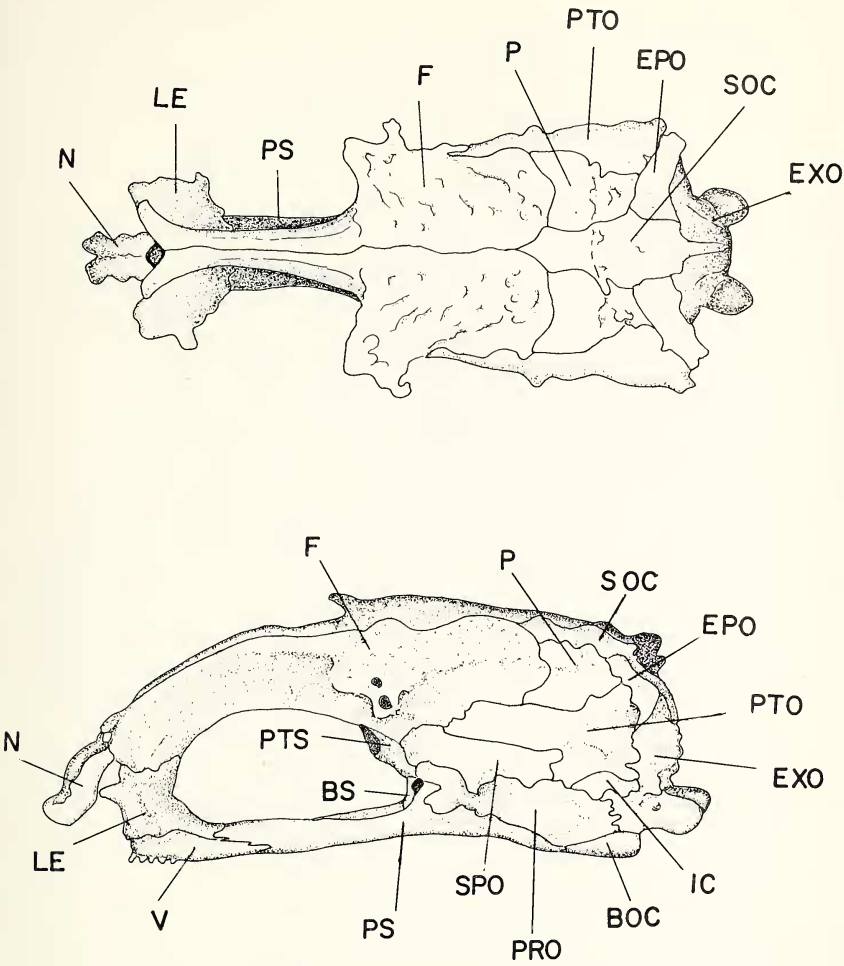
Holotype: LACM 32551-34, a 62.5 mm ♂ from an isolated rockpile 1.4 miles NW of Isla del Caño, Costa Rica. Taken with rotenone in 65'-75' (21-24 m) by William Bussing, John McCosker, James McLean, Manuel Murillo, Richard Rosenblatt and Richard Wheeler on 16 March 1972.

Paratypes: Costa Rica: LACM 32551-35, 403 (18-70 mm), bearing the same data as the holotype; USNM 214706, 10, bearing the same data as holotype; SIO-75-404, 255 (21.5-62), Isla del Caño. Panama: Golfo de Chiriqui: SIO70-358, 14 (22-65 mm), Isla Montuosa; SIO71-51, 6 (30-60 mm), SIO71-37, 2 (42-46 mm), Isla Uva; SIO71-54, 1 (38), Isla Canal de Afuera.



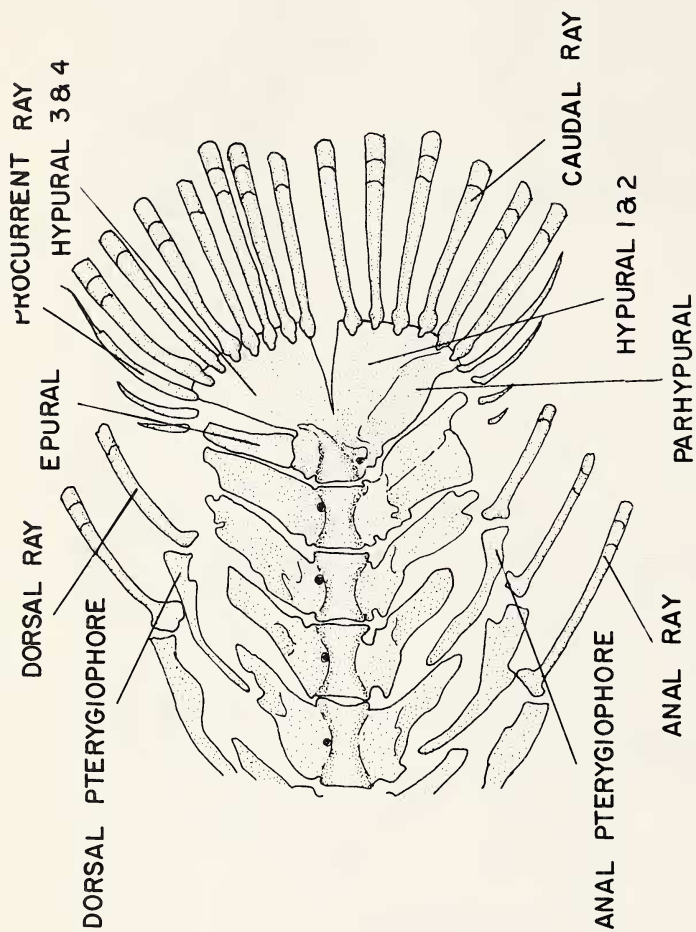
M. SANDAE

FIGURE 3. Cranial skeleton, *Mccoskerichthys sandae* (SIO70-358)



M. SANDAE

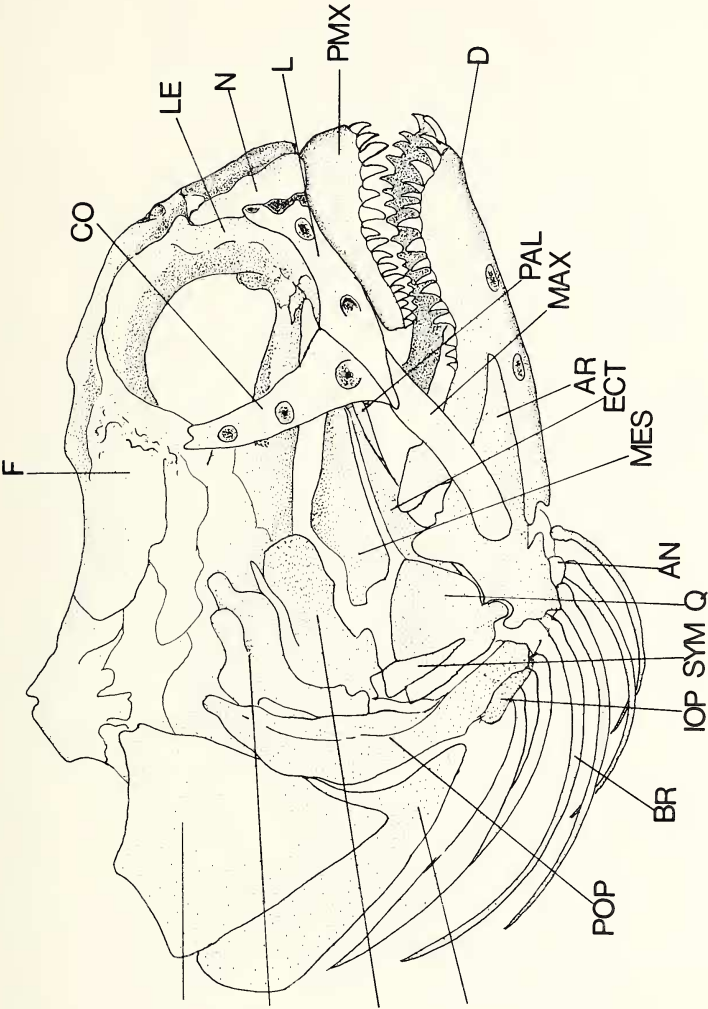
FIGURE 4. Neurocranium, *Mccoskerichthys sandae* (SIO70-358)



M. SANDAE

CAUDAL

Caudal skeleton, *Mccoskerichthys sandae* (SI070-358)



P. BICIRRIS

FIGURE 6. Cranial skeleton, *Protentemaria bicirris* (UCLA 65-71)

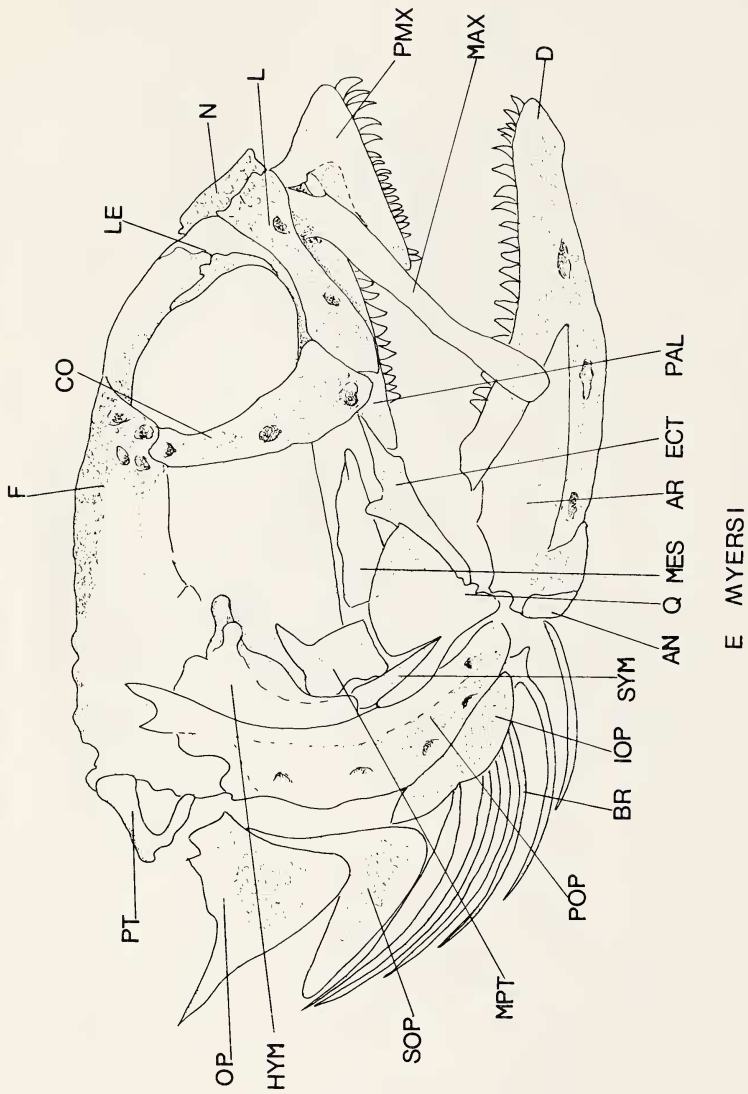
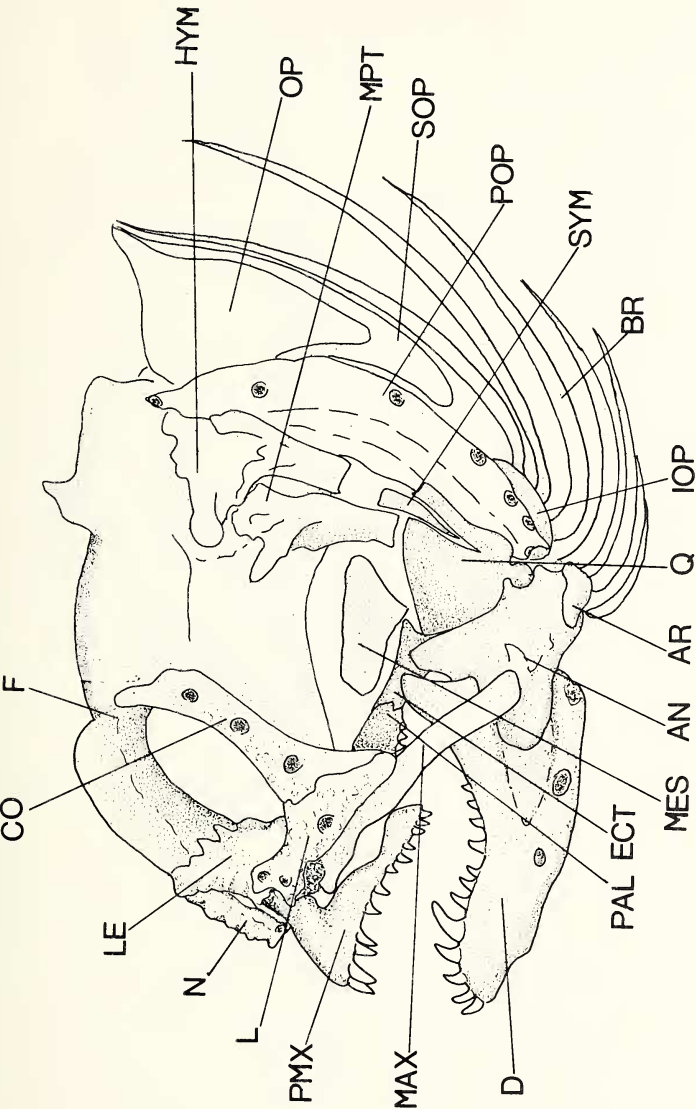
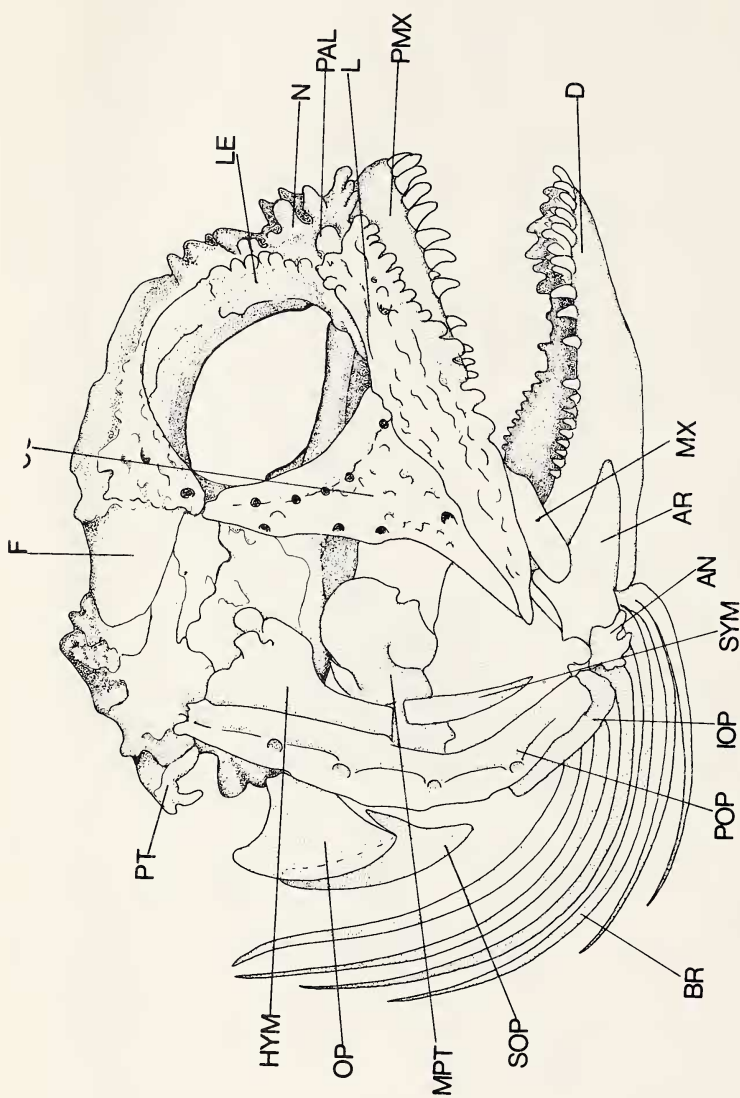


FIGURE 7. Cranial skeleton, *Ekemblemaria myersi* (UCLA 53-86)



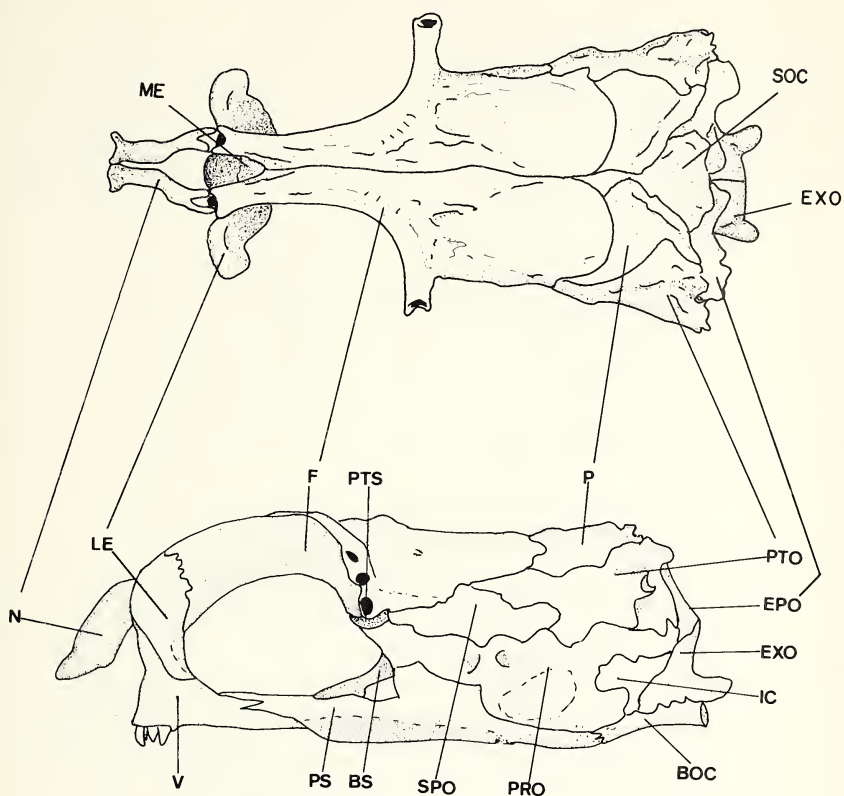
C ANGELICA

FIGURE 8. Cranial skeleton, *Coralliozetus angelica* (right side damaged) (UCLA 65-86)



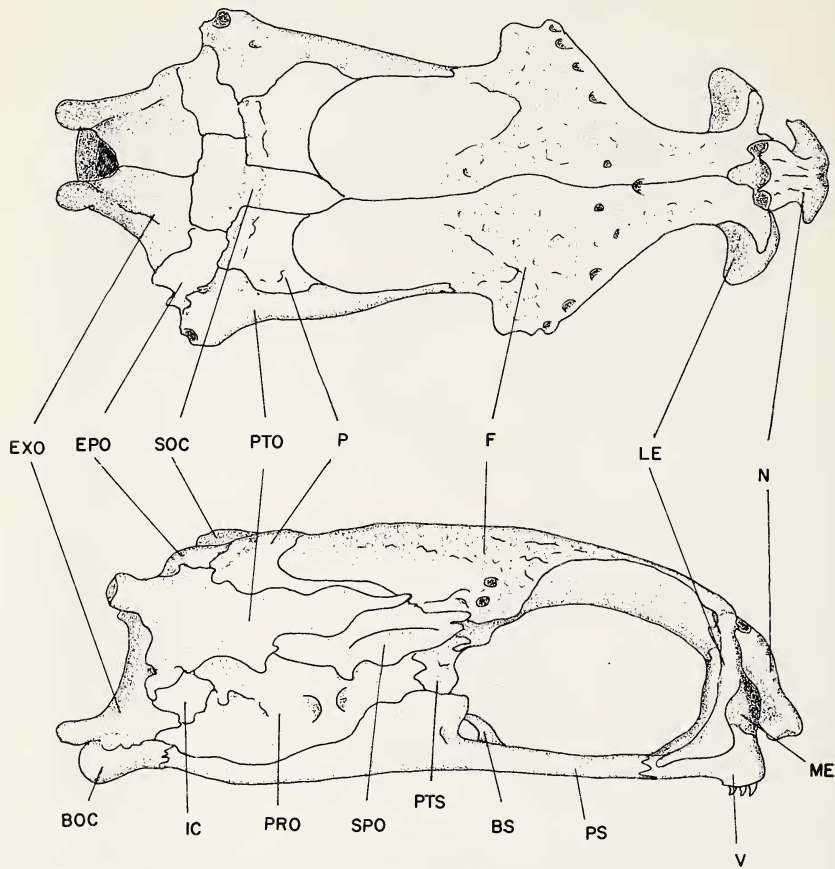
A. CASTROI

FIGURE 9. Cranial skeleton, *Acanthemblemaria castroi* (UCLA 64-33)



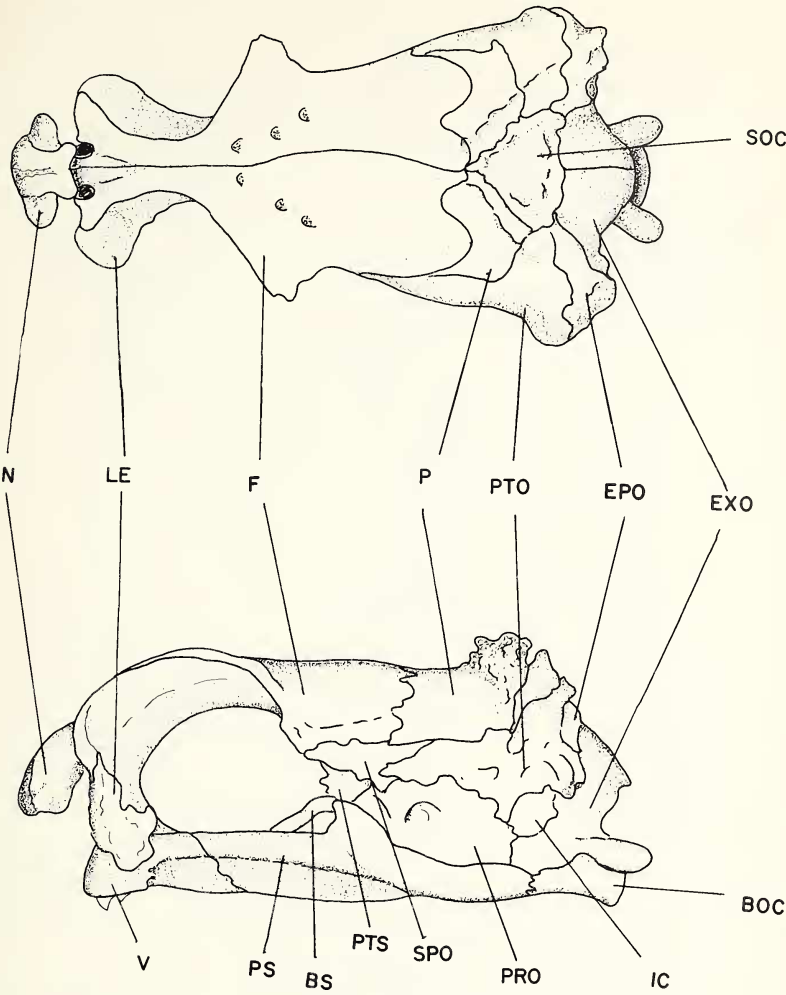
P. BICIRRIS

FIGURE 10. Neurocranium of *Prottemblemaria bicirris* (UCLA 65-71)



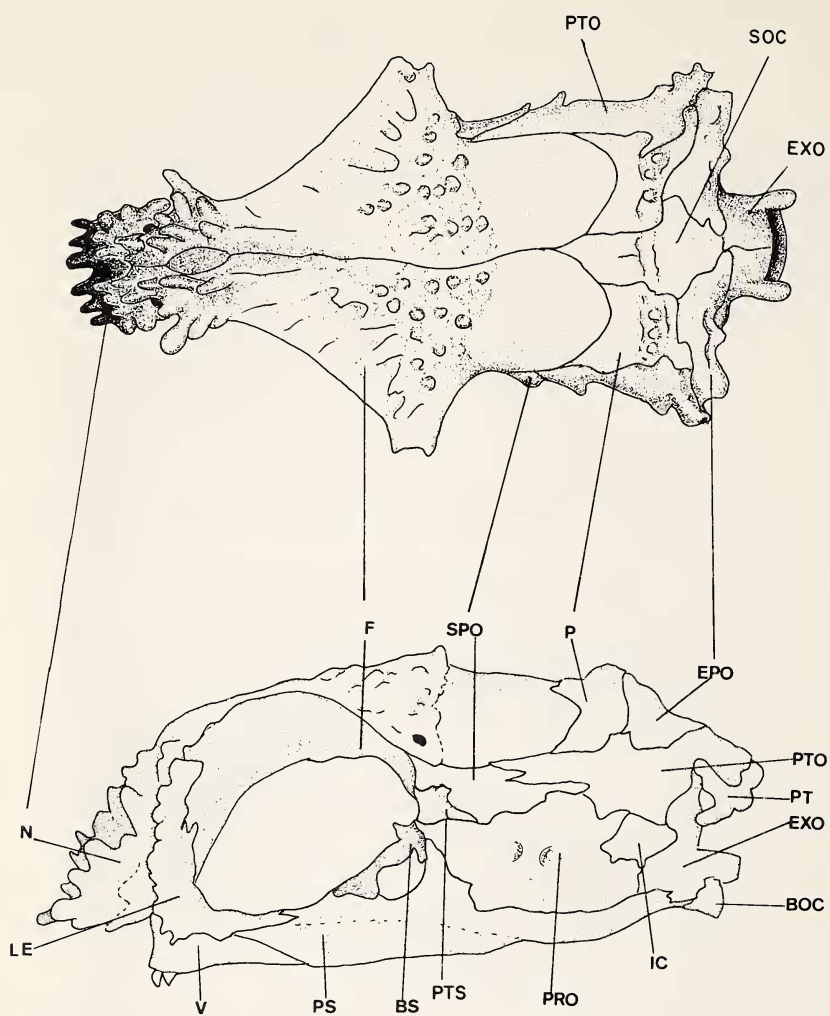
E MYERSI

FIGURE 11. Neurocranium of *Ekemblemaria myersi* (UCLA 53-86)



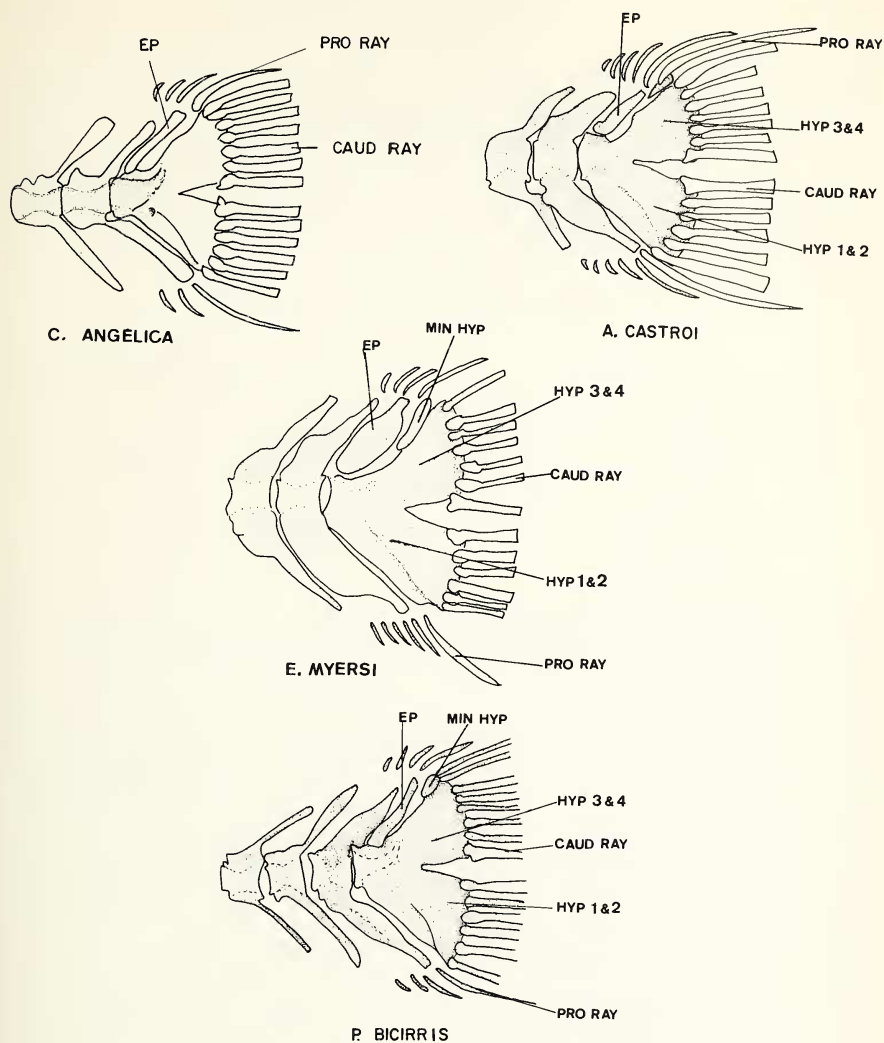
C ANGELICA

FIGURE 12. Neurocranium of *Coralliozetus angelica* (UCLA 65-86)



A. CASTROI

FIGURE 13. Neurocranium of *Acanthemblemaria castroi* (UCLA 64-33)



CAUDALS

FIGURE 14. Comparative caudal skeletal anatomy, *Protemblemaria* to *Acanthemblemaria* line.

ACKNOWLEDGMENTS

The Costa Rica collections were made possible by the Janss Foundation; the Panama collections were made from the R/V *ALPHA HELIX*.

The illustration of the holotype was drawn by Brian Burnette. The osteological drawings are by Stephens except for figure 6 by Cassie Cussik. The osteological portion of this study was partially supported by National Science Foundation Grant GB27266 to Stephens.

A NOTE ABOUT FIGURES AND LEGENDS

The osteological figures do not attempt to illustrate all sensory pores. The following abbreviations are used in the osteological illustrations.

AN, Angular; AR, Articular; BOC, Basioccipital; BR, Branchiostegals; BS, Basisphenoid; CO, Circumorbital; D, Dentary; ECT, Ectopterygoid; EPO, Epiotic; EXO, Exoccipital; F, Frontal; HYM, Hyomandibular; IC, Intercalar; IOP, Interopercular; L, Lachrymal; LE, Lateral ethmoid; MPT, Metapterygoid; MSPT, Mesopterygoid; MX, Maxilla; N, Nasal; OP, Opercular; P, Parietal; PAL, Palatine; PMX, Premaxilla; POP, Preopercular; PRO, Prootic; PS, Parasphenoid; PTO, Pterotic; PTS, Pterosphenoid; Q, Quadrate; SOC, Supraoccipital; SOP, Subopercular; SPO, Sphenotic; SYM, Symplectic; V, Vomer.

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